

ANTS PROVIDE SUBSTRATE FOR EPIPHYTES

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ABSTRACT. Two classes of ant–epiphyte relationships have drawn the attention of naturalists: epiphytes that provide chambers within which ants nest (domatia), and ants that plant epiphyte seeds in carton nests, producing “ant gardens.” Ants are major movers and formers of organic matter in the canopies of lowland tropical forests, and ant derived accumulations of organic matter provide substrate for the establishment of many vascular epiphytes. This very general relationship may lead to some epiphyte species becoming specialized ant associates, either as components of ant gardens or as epiphytes providing domatia. In only one case is there evidence that coevolution has occurred. Epiphytes appear to have evolved specific adaptations for life with ants, but rarely have ants been shown to have specific adaptations to epiphytes.

The earliest European observers of tropical plant life recorded species of epiphytes that produced peculiar swellings or chambers (historical review in Huxley, 1978). They also noticed that these chambers often contained biting ants. Such observations of ant–plant relationships have captured the attention of biologists and have produced a voluminous literature filled with lively debate over the nature of the relationships (reviews in Bequaert, 1922; Janzen, 1974; Huxley, 1980; Buckley, 1982). In this paper ant–epiphyte relationships are briefly reviewed. The production of carton by ants, an overlooked and underestimated source of epiphyte substrate, and the coevolution between ants and epiphytes are discussed.

ANT–EPIPHYTE RELATIONSHIPS

Domatia

Natural plant cavities that ants inhabit are called domatia (Wilson, 1971). The tropics of the Far East are the richest in domatia-producing epiphytes (Janzen, 1974; Huxley, 1980), the main genera being *Hydnophyllum*, *Myrmecodia* (Rubiaceae; Treub, 1883a, 1888; Janzen, 1974; Huxley, 1978), *Dischidia* (Asclepiadaceae; Treub, 1883b; Groom, 1893; Scott & Sargent, 1893; Thiselton-Dyer, 1902; Janzen, 1974), and *Lecanopteris* (Polypodiaceae; Yapp, 1902; Janzen, 1974; Jermy & Walker, 1975). In the New World tropics, a few domatia-producing epiphytes are also found, including the genus *Solanopteris* (Polypodiaceae; Gomez, 1974, 1977), species of *Tillandsia* (Bromeliaceae; Wheeler, 1942; Benzing, 1970), and *Schomburgkia* (Orchidaceae; Bequaert, 1922).

The relationship between ants and epiphytes is often considered a mutualism: the ants benefit from sheltered nest sites and the plants benefit from the nutrients that the ants gather and concentrate in their nests. Benefits to the epiphytes

have been supported by morphological and experimental evidence. *Myrmecodia*, *Hydnophyllum*, *Dischidia*, and *Lecanopteris* all have domatia with darkly pigmented inner surfaces, interior absorptive tissue, and narrow tunnel-like entrances which are directed downward or toward the substrate (Janzen, 1974; Huxley, 1980). The ants in these domatia deposit nutrient-rich refuse and fecal material on the absorptive regions (roots proliferate and penetrate the refuse pile in the case of *Dischidia*; Janzen, 1974). Radioisotope studies have shown that the nutrients are absorbed and incorporated by *Myrmecodia* and *Hydnophyllum* (Huxley, 1978; Rickson, 1979). Benzing (1970) similarly showed absorption of nutrients inside domatia of ant-inhabited *Tillandsia*.

Ant Gardens

Although epiphyte domatia are rare in the neotropics, a different ant–epiphyte relationship is more common. Ule (1901, 1905, 1906) observed that certain ant nests in Brazil sprouted a characteristic set of epiphytes. The nests were composed of accumulated organic material perched in trees, and the roots of the epiphytes filled the core of the nests, making them quite sturdy. He called these ant-associated clumps of epiphytes “ant gardens.” The plants he found were mainly in the Araceae, Gesneriaceae, and in the genus *Peperomia* (Piperaceae), and the dominant epiphytes were specialized species that only occurred on ant gardens. Ule reported observing ants gathering and planting epiphyte seeds in the walls of these nests, and made the conjecture that ant gardens were initiated in this way. Wheeler (1921) made additional observations on ant gardens in Guyana, and he concluded that Ule was incorrect; ants were simply occupying preexisting clumps of epiphytes. Davidson (pers. comm.) has confirmed Ule’s original conjecture, and shown that ant garden epiphytes, in contrast to many

free-living epiphytes, have seeds with chemical ant attractants, and that ants harvest these seeds and incorporate them into their nest walls. The ant genera *Anochetus*, *Odontomachus*, *Crematogaster*, *Dolichoderus*, *Azteca*, *Camponotus* (Wheeler, 1942), *Pheidole*, and *Cyphomyrmex* (pers. obs.) contain species that have been observed living in ant gardens.

I propose that ant gardens are the most obvious manifestation of a widespread and general use of ant nests by epiphytes. Ants may be major providers of epiphyte substrate and major initiators of epiphyte growth in many tropical rainforests.

Carton Nests

Ants form nests above the ground in various ways (Wheeler, 1910). Ants commonly nest in preformed cavities or cavities they themselves excavate in dead wood. Many species build their own nests out of accumulated and molded organic material. The nature of this material is variable; it can be thin and parchment-like, hard and brittle, coarse and flexible but still in the form of distinct walls, or a more solid mass of soft material with ramifying ant galleries inside. Nests made of the latter material are often called "earthen nests," while nests of the former materials are called carton nests. All such material is referred to as carton in this paper. The cement used to hold the accumulated material together is thought to be a secretion of the ants' maxillary glands (Wheeler, 1910). The environmental origin of the accumulated material is usually unknown. Coarser cartons are clearly composed of plant fibers, and on occasion ants may scrape material from tree bark (pers. obs.). Carton nests may occur appressed to tree trunks, lodged in forks, suspended from or wrapped around small branches, around bunched leaves at the ends of branches, or even on the undersurfaces of individual leaves. Ants use carton not only to build nest sites, but also to shelter scale insects which they tend for honeydew. Carton construction is widespread among the ants; in the neotropics many of the larger genera contain species that build arboreal carton nests.

In lowland rainforests of Costa Rica (0–500 m elevation), ant carton is often colonized by a variety of epiphytes. The appearance of these ant-epiphyte associations varies from spatially discrete, globular ant gardens to diffuse layers of epiphyte-sprouting carton.

Azteca spp. and *Crematogaster* cf. *montezumia* form the most discrete ant gardens in Costa Rica. The colonies occur as clusters of globular carton nests, each with a bushy growth of epiphytes. The nests and many smaller satellite shel-

ters cover dense populations of scale insects. The scale insects are probably the major food supply for the ants. *Crematogaster limata* subsp. *parabiotaica*, although often found in ant gardens with other ant species (Wheeler, 1921; Weber, 1943), may not construct ant gardens on its own (Davidson, pers. comm.).

Kleinfeldt (1978) studied the relationship between a carton-building ant, *Crematogaster longispina*, and the epiphyte *Codonanthe crassifolia* (Gesneriaceae) at a lowland site in Costa Rica. Individual plants on *Crematogaster* nests were healthy and growing, while those not on nests looked unhealthy and were not growing. Her observations suggested that *C. crassifolia* was an obligate associate of ant nests and that those plants without nests were relicts following nest abandonment and carton disintegration.

Crematogaster longispina's relationships with epiphytes are not isolated situations, nor restricted to *Codonanthe crassifolia* (pers. obs.). This ant species occurs throughout the Atlantic rainforest of Costa Rica. In many sites, it is a dominant component of the forest understory. It has large diffuse colonies living in many small carton nests. *Crematogaster longispina* is a prodigious builder of loose, coarse-fibered carton, making carton for nests, shelters over scale insects, and galleries to connect all the parts. The bulk of this carton is usually layered under and around the roots and stems of aroids and gesneriads that run up and down tree trunks. Where new carton is being made, there is usually a flush of newly sprouted epiphytes in the walls.

The following is an example of a very diffuse ant-epiphyte association, in which carton construction was only a small part of the ant nest, and there was no indication that the associated epiphyte was specialized for life with ants. A species of *Crematogaster* (cf. *brevispinosa*) was observed in Corcovado National Park, in the crown of a *Protium* tree. The bulk of the colony occupied chambers inside living branches, and carton galleries extended along the branches between entrances. The ant carton contained newly sprouted *Peperomia* seedlings, and a temporal progression from bare new carton, to carton with seedlings of *Peperomia*, to bushy *Peperomia* growth on older, moss-covered carton was obvious. Branches without ants lacked epiphyte growth.

From Kleinfeldt's (1978) study and various reports of ant gardens, one has the impression that ant-epiphyte associations are specialized and spatially restricted phenomena which are interesting from an evolutionary point of view, but not of major ecological importance. My observations on the abundance of carton accumulated by ants and the use of that carton by epiphytes,

however, have led me to consider ant-epiphyte relationships in a new light. Epiphytes are often patchily distributed in rainforest canopies. Some trees have largely clean branches with scattered bromeliads and orchids, while other trees are heavily covered with clumps of aroids, gesneriads, and *Peperomia*. Orchids and bromeliads typically establish on bare substrate, but many other vascular epiphytes appear to require an initial accumulation of organic matter. Once epiphytes are established, they are traps for and generators of additional organic matter, creating a positive feedback for epiphyte growth. Initial establishment, however, may be very often due to ants. Thus, in lowland rainforest, ants may greatly influence epiphyte distribution and rate of colonization.

COEVOLUTION BETWEEN ANTS AND EPIPHYTES

Has coevolution occurred between epiphytes and ants? Coevolution between two species is often inferred when each species exhibits novel adaptations pertaining to some trait of the other (Futuyma & Slatkin, 1983). For example, certain ants within the genus *Pseudomyrmex* will nest only in certain species of *Acacia*, which they aggressively defend, and the *Acacia* species have swollen-thorn domatia, extrafloral nectar glands, and proteinaceous food bodies for the ants (Janzen, 1966). It is clear that some epiphytes have specialized adaptations for ants, but what traits do ants exhibit that are specific to epiphytes?

Among the many reports of ants associated with epiphytes (Bequaert, 1922; Wheeler, 1942), three groups have received the most attention: (1) *Iridomyrmex myrmecodiae* and relatives in the domatia-producing epiphytes of the Old World (Janzen, 1974; Huxley, 1980), (2) *Azteca olitrix*, *A. trailii*, and *A. ulei* which occur in ant gardens (Ule, 1905, 1906), and (3) *Crematogaster limata* subsp. *parabiotica* and *Camponotus femoratus* which also occur in ant gardens (Wheeler, 1921). Janzen (1974) described several features of *Iridomyrmex myrmecodiae* that appear to be special adaptations to living in Southeast Asian myrmecophytes. The ants pack nutrient-rich debris into special absorptive chambers of the myrmecophytes, in contrast to other arboreal ants which typically eject debris from the nest. In addition, the debris is very rich in dead insect parts, richer than would be expected for refuse piles, and so the ants may be directly enhancing the nutrient level of the debris which they pack into the chambers.

Neotropical ant gardens are formed by many species of ants and plants, and the associations are not very specific (Buckley, 1982). Observa-

tions of ants that form ant gardens have not revealed special adaptations that suggest coevolution with epiphytes. The basic behaviors seen in ant garden formation—carton construction and the harvesting and planting of epiphyte seeds—are not sufficient indicators of special adaptation.

Carton construction by ants cannot be viewed as a specialized adaptation to life with epiphytes; it is too widespread and too often found without associated epiphytes. It may be argued that epiphytes on carton nests benefit ants by strengthening the nest, but ants can make very strong, durable carton in the absence of epiphytes. Epiphytes may even be detrimental by decreasing temperature-dependent larval growth by overshadowing, and eventually making the nest uninhabitable as the roots fill the interior. No evidence exists to support either view.

The fact that ants harvest epiphyte seeds and incorporate them into their nest walls cannot be used to infer special adaptation. Carton-building ants often incorporate nest refuse into their carton, and seed planting may result from this generalized behavior. Attraction to seed odor is not necessarily a special adaptation either. Myrmecochory, the dispersal of seeds by ants, is a common phenomenon in which seeds produce a food-body or some other attraction that causes ants to carry the seeds back to their nests (Horvitz, 1981). The ants involved are generalized foragers, and no special adaptation of ants to seed-harvesting is implied. To demonstrate special adaptation of ants to epiphytes, one must show that attraction to epiphyte seeds is novel, and not dependent on a preexisting ant behavior. Also, in field trials of ant attraction to seeds, the effects of conditioning should be carefully controlled.

Given the abundance of ant carton, with its moisture holding capacity and its potential high nutrient status, it is not surprising that many epiphyte species have evolved specializations for being buried in it. One can imagine an evolutionary sequence in which ant attractive seeds are evolved first, as a means of being incorporated into new ant carton. In the case of the Southeast Asian myrmecophytes, domatia with internal absorptive tissue may then have evolved, improving access to ant-derived nutrients and causing a longer residence time of an associated ant colony.

CONCLUSIONS

The abundant carton produced by ants in tropical wet forests may greatly influence epiphyte establishment and growth, and many epiphytes have evolved special adaptations for close association with ants. Although future taxonomic and behavioral studies of ants may reveal species

with specialized adaptations for life with epiphytes, in many cases ants may not be coevolutionary partners, but rather a more stable biotic component of the environment to which epiphytes have evolutionarily responded.

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